Observations on the Food and Feeding of some Vermivorous *Conus* on the Great Barrier Reef

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(2 Text figures)

INTRODUCTION

The feeding mechanism of post-larval *Conus* is well documented (for references see Kohn, 1959, 1968). As far as is known, all species are carnivorous and possess a venom apparatus used primarily in the capture of prey. Kohn (1959) has shown that three groups of species within the genus can be distinguished on the basis of their food. Most feed on marine worms, mainly polychaetes, while the second group feeds on fish and the third on other gastropods. Although details of the food of *Conus* from several parts of the Indo-Pacific are known (Kohn 1956, 1959, 1960, 1966, 1968), little information is available on the diet of *Conus* on the Great Barrier Reef. Details of the feeding, food, and degree of dietary specialization for some of the most common intertidal vermivorous species are investigated in this study, as this information was considered basic to subsequent work on the effects of the venoms of these species.

STUDY AREAS

This report is based on field studies made at Lady Elliot Island and Low Isles. Lady Elliot Island (24°07′ S and 152°45′ E) is a shingle cay situated at the southern extremity of the Great Barrier Reef and about 40 miles from the Queensland mainland. Only populations of *Conus* which occur on the reef crest have been studied. The reef crest area is exposed at low tides except extreme low water neaps. Studies were made of specimens of *Conus* collected from the reef to the south-east, east and north of the island where the crest is conspicuous and easily defined. These areas are very flat and composed principally of shingle covered by algal turf. Distributed erratically over the crest are boulders and shallow sand-filled depressions.

Low Isles (16°23′ S and 145°34′ E) is approximately 7 miles off the North Queensland coast and about 20 miles shoreward of the outer Barrier Reefs. Several publications may be consulted to give details of the reef at Low Isles (e. g. Stephenson *et al.*, 1931; Stephenson, Endean & Bennett, 1958). Specimens were collected from the reef on the south-east (see Stephenson, Endean & Bennett, *op. cit.*: 265, fig. 2, locality 31) at low water spring tides. The habitat was more complex than that described above at Lady Elliot Island because the area exposed at low tide included some living coral colonies on the seaward margin of the crest.

METHODS

Lady Elliot Island was visited twice in 1967 – from 23rd February to 7th March and from 29th June to 5th July. Low Isles was visited from 22nd to 29th of August 1969. Specimens of the most common species of *Conus* were collected on day and night low tides, weather permitting, and placed in 10% formalin immediately after collection. The shell length of each specimen was measured to the nearest 0.5 mm with vernier calipers and the gut contents examined within 24 hours of collection. As polychaetes were the main prey items, indigestible setae and jaws permitted subsequent identification by referring to Day,

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1967; Fauvel, 1923, 1927; and Monro, 1931. References to the other pertinent literature used, such as species descriptions, are listed in the above monographs.

Information theory may be used to derive numerical measures of prey species diversity and prey specificity. Following Kohn (1966, 1968) Shannon & Weaver's (1949) entropy (H) was used as a measure of prey species diversity. When all prey species are equally abundant H is a maximum of ln N (N being the number of prey species identified). H is always non-negative and is zero when only one prey species is present. Redundancy (R) (Shannon & Weaver, *op. cit.*) may be used as a direct measure of relative food specialization (H. S. Horn, unpublished, cited by Kohn, 1966). When each item in a diet is equally abundant $R = 0$. As the diet becomes increasingly specialised R approaches 1.

The food species overlap index R_o (Horn, 1966) was used as a measure of prey species overlap. R_o varies from 0 when two predatory species have completely distinct diets to 1 when the diets are identical with respect to prey species composition and proportion.

RESULTS

(1) SPECIES COLLECTED

Lady Elliot Island

The following species were collected alive on the reef crest at Lady Elliot Island during the two trips in 1967:

Conus aulicus Linnaeus, 1758
Conus catus Hwass in Bruguière, 1792
Conus chaldeus Röding, 1798
Conus coronatus Gmelin, 1791
Conus ebraeus Linnaeus, 1758
Conus episcopus Hwass in Bruguière, 1792
Conus flavidus Lamarck, 1810
Conus geographus Linnaeus, 1758
Conus imperialis Linnaeus, 1758
Conus lividus Hwass in Bruguière, 1792
Conus marmoreus Linnaeus, 1758
Conus miliaris Hwass in Bruguière, 1792
Conus musicus Hwass in Bruguière, 1792
Conus omaria Hwass in Bruguière, 1792
Conus rattus Hwass in Bruguière, 1792
Conus sanguinolentus Quoy & Gaimard, 1834
Conus striatus Linnaeus, 1758
Conus terebra Born, 1780
Conus textile Linnaeus, 1758
Conus tulipa Linnaeus, 1758
Conus virgo Linnaeus, 1758

Low Isles

The following species were collected alive by the author on the reef crest at Low Isles during August 1969.

Conus capitaneus Linnaeus, 1758
Conus chaldeus Röding, 1798
Conus coronatus Gmelin, 1791
Conus ebraeus Linnaeus, 1758
Conus emaciatus Reeve, 1849
Conus flavidus Lamarck, 1810
Conus frigidus Reeve, 1848
Conus lividus Hwass in Bruguière, 1792
Conus marmoreus Linnaeus, 1758
Conus miliaris Hwass in Bruguière, 1792
Conus musicus Hwass in Bruguière, 1792
Conus sanguinolentus Quoy & Gaimard, 1834
Conus rattus Hwass in Bruguière, 1792

For the purposes of this paper Cernohorsky (1965) has been followed in considering *Conus lividus* and *C. sanguinolentus* as separate species. Kohn (1959a) considers *C. sanguinolentus* to be synonymous with *C. lividus*.

(2) SIZE AND SEX RATIOS

Shell length was used as a measure of shell size. Information on the size and sex of the dissected specimens of the commoner species is summarised in Figures 1 and 2. These figures are not a measure of the relative abundance of the *Conus* species on the reef crest.

Shell length of males and females does not differ at the 0.05 level of significance in any species tested at Lady Elliot Island or Low Isles (t tests). The sex ratio differs significantly from unity only for *Conus sanguinolentus* at Lady Elliot Island (X^2 test $0.001 < P < 0.05$).

(3) FEEDING OBSERVATIONS

During dissection of *Conus* the position of food in the gut was noted, and as the time of collection was known approximate feeding times could be ascertained. Kohn (1959) showed that for the vermivore, *C. abbreviatus* Reeve, 1843, food started to move into the intestine after

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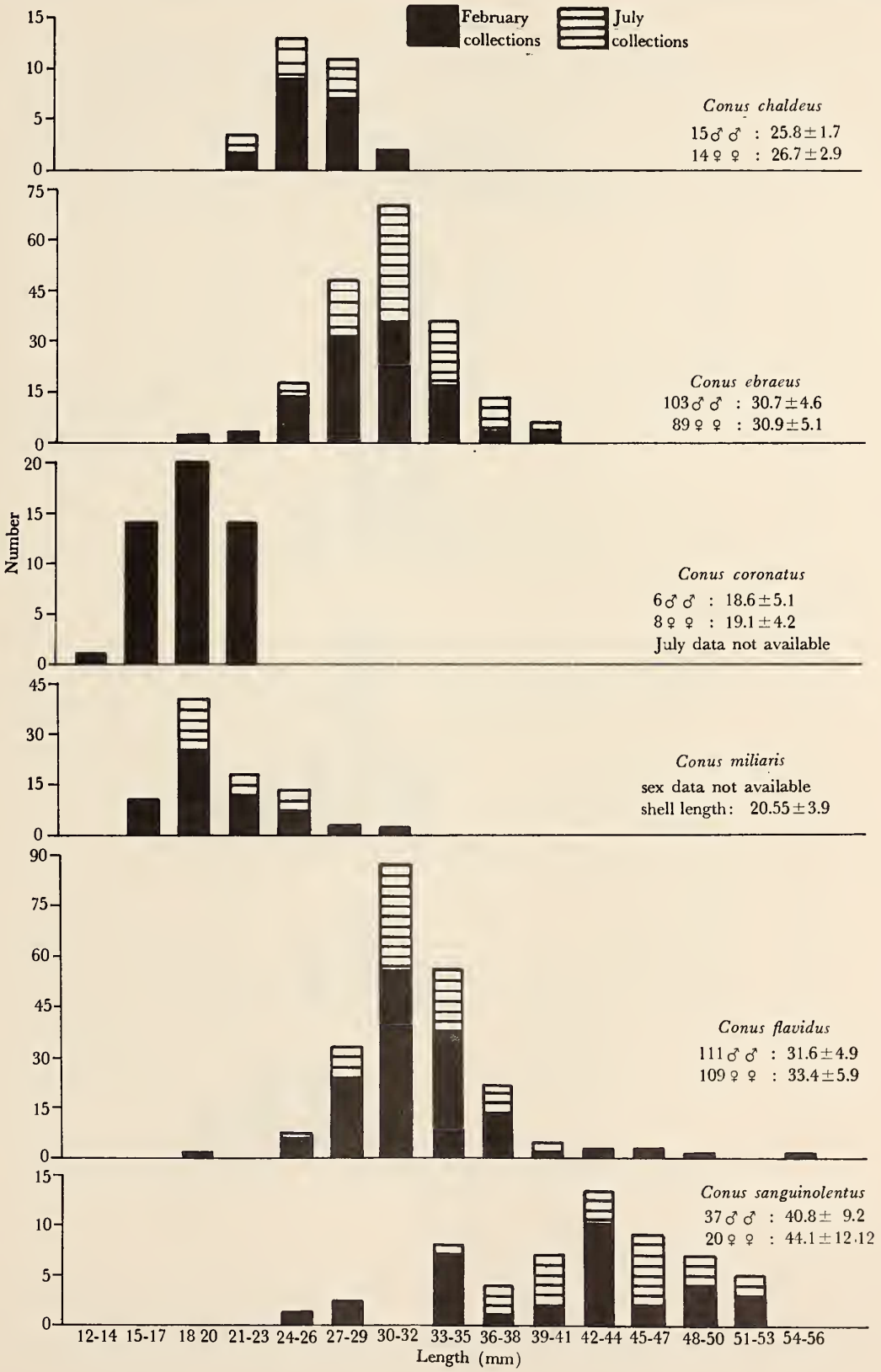
Figure 1

Length frequency distributions for *Conus* collected at Lady Elliot Island.
Sample size, mean shell length ± standard deviation are given for both sexes. For this February and July data are combined.


February collections
July collections
Conus chaldeus
15♂♂ : 25.8±1.7
14♀♀ : 26.7±2.9
Conus ebraeus
103♂♂ : 30.7±4.6
89♀♀ : 30.9±5.1
Conus coronatus
6♂♂ : 18.6±5.1
8♀♀ : 19.1±4.2
July data not available
Conus miliaris
sex data not available
shell length: 20.55±3.9
Conus flavidus
111♂♂ : 31.6±4.9
109♀♀ : 33.4±5.9
Conus sanguinolentus
37♂♂ : 40.8± 9.2
20♀♀ : 44.1±12.12
Number
12-14 15-17 18 20 21-23 24-26 27-29 30-32 33-35 36-38 39-41 42-44 45-47 48-50 51-53 54-56
Length (mm)

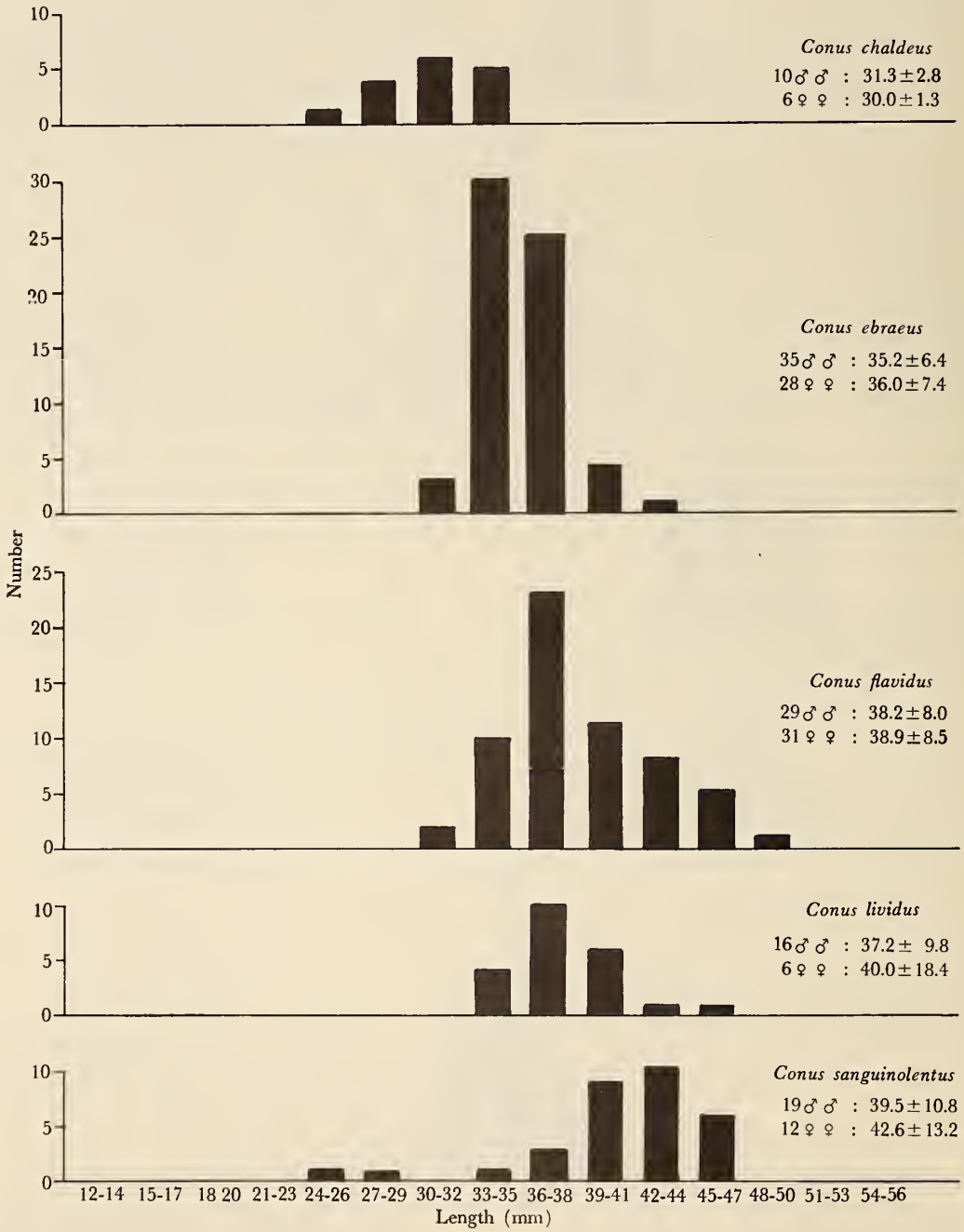

Conus chaldeus
10♂♂ : 31.3±2.8
6♀♀ : 30.0±1.3
Conus ebraeus
35♂♂ : 35.2±6.4
28♀♀ : 36.0±7.4
Conus flavidus
29♂♂ : 38.2±8.0
31♀♀ : 38.9±8.5
Conus lividus
16♂♂ : 37.2± 9.8
6♀♀ : 40.0±18.4
Conus sanguinolentus
19♂♂ : 39.5±10.8
12♀♀ : 42.6±13.2
Number
12-14 15-17 18 20 21-23 24-26 27-29 30-32 33-35 36-38 39-41 42-44 45-47 48-50 51-53 54-56
Length (mm)

Table 1

Percentage of *Conus ebraeus* which had food in the proboscis and oesophagus at different times of day. Low tide occurred at about the middle of each collecting period. Average times of sunset and sunrise for each collecting trip are indicated.

Lady Elliot Island February-March Sunrise: 0540 Sunset: 1825			Lady Elliot Island June-July Sunrise: 0635 Sunset: 1710			Low Isles August Sunrise: 0631 Sunset: 1815		
Time	Number collected	% with food in proboscis & oesophagus	Time	Number collected	% with food in proboscis & oesophagus	Time	Number collected	% with food in proboscis & oesophagus
0130-0300	41	2.4	0000-0200	10	40			
0300-0500	17	29.4						
0600-0900	61	39.3						
			0800-1000	19	68.4			
			1000-1200	19	36.8	0930-1230	50	18
			1200-1500	28	32	1300-1500	14	0
			2000-2300	22	4.6			

Table 2

Percentage of *Conus flavidus* which had food in the proboscis and oesophagus at different times of day. Low tide occurred at about the middle of each collecting period. Average times of sunset and sunrise for each collecting trip are indicated.

Lady Elliot Island February-March Sunrise: 0540 Sunset: 1825			Lady Elliot Island June-July Sunrise: 0635 Sunset: 1710			Low Isles August Sunrise: 0631 Sunset: 1815		
Time	Number collected	% with food in proboscis & oesophagus	Time	Number collected	% with food in proboscis & oesophagus	Time	Number collected	% with food in proboscis & oesophagus
0130-0500	95	16	0000-0400	23	34.8	0410-0240	9	22.2
0600-0915	61	26.2						
			0800-1200	24	0	0930-1230	41	2.4
			1200-1400	16	12.5	1300-1500	15	6.7
1500-1700	6	0						
			2000-2200	16	6.3			
			2200-2300	6	83.3			

(⟵ on facing page)

Figure 2

Length frequency distributions for *Conus* collected at Low Isles.
Sample size, mean shell length ± standard deviation are given for both sexes.

$1\frac{1}{2}$ hours in the oesophagus. After 3 hours faecal matter appeared in the rectum. Thus, food in the oesophagus and proboscis suggests recent feeding. Tables 1 and 2 summarise these data for *C. ebraeus* and *C. flavidus,* the species for which most information is available.

These data do not cover the full 24 hour period and are limited to low tide times. However, it can be seen from

Tables 1 and 2 that *Conus flavidus* appears to feed mainly at night while the *C. ebraeus* feeding time extends at least until mid-morning. In 2 cases collecting of *C. ebraeus* before 0300 hours yielded very low returns. Collections between midnight and dawn for both species produced a higher percentage of food in the proboscis and oesophagus during winter than in summer which suggests that the onset of feeding activity may be linked to sunrise and sunset times.

Although the capture of a prey worm by *Conus* was never observed, *C. ebraeus* and *C. flavidus* were often seen at night with proboscis extended and probing the algal turf which covers the crest area. *Conus ebraeus* and *C. flavidus* were each seen once while swallowing their prey, *Palola siciliensis* and *Dasybranchus cadacus* respectively. In neither case was there any evidence of prey paralysis. On three occasions active non-paralysed prey was found in the oesophagus of *Conus*. Two specimens of live *D. cadacus* were removed each from a *C. flavidus* and a live *P. siciliensis* was removed from *C. ebraeus*.

(4) FOOD

Tables 3 and 4 show the food items identified from *Conus* collected at Lady Elliot Island and Low Isles respectively. All species fed exclusively on polychaetes except *C. sanguinolentus* which ate enteropneusts as well. Errant polychaetes of the families Eunicidae and Nereidae were the most important items in the diets of *C. chaldeus,*

Table 3

Prey organisms consumed by the six most common species of vermivorous *Conus* on the reef crest at Lady Elliot Island. February-March and June-July data are combined.

Prey organisms	*Conus* species and number of individuals examined					
	chaldeus 29	*ebraeus* 192	*coronatus* 96	*miliaris* 85	*flavidus* 220	*sanguinolentus* 57
A Polychaetes						
Ampharetidae (1 species)					1	
Capitellidae						
Dasybranchus cadacus (Grube, 1846)		1			35	
other capitellids (1 species)					1	
Cirratulidae (1 species)						4
Maldanidae						
Petaloproctus terricola Quatrefages, 1865 [1]					4	
Axiothella australis Augner, 1914 [1]					7	
Terebellidae						
Strebolosoma (2 species)					3	
Eunicidae						
Palola siciliensis Grube, 1840	2	37	2	4	1	
Palola siciliensis Grube, 1840 [1]		25	3	7	1	
Arabella irecolor (Montagu, 1804)			3			
Lysidice collaris Grube, 1870		1	9	8		
Nereidae						
Perinereis (1 species)		3				
other nereids		3	1			
Phyllodocidae (1 species)						2
unidentified annelids	5	13	7	3	16	2
B Enteropneusts						
Ptychoderidae						
Ptychodera flava Eschscholtz, 1825 [1]						5
Total identified food	7	83	25	22	69	13
Unidentified food	0	5	0	0	26	1

[1] tentative identification

Table 4

Prey organisms consumed by vermivorous *Conus* on the reef crest at Low Isles.

	Conus species and number of individuals examined						
	chaldeus 16	*ebraeus* 63	*miliaris* 9	*rattus* 7	*flavidus* 60	*lividus* 22	*sanguinolentus* 31
A Polychaetes							
Capitellidae							
Dasybranchus cadacus (Grube, 1846)					1		
Cirratulidae (1 species)							1
Maldanidae (1 species)						1	
Terebellidae							
Thelepus setosus (Quatrefages, 1865)						1	
Eunicidae							
Palola siciliensis Grube, 1840	5	5					
Eunice antennata (Savigny, 1820)				2			
Lysidice collaris (Grube, 1870)			1				
unidentified eunicid		1					
Nereidae							
Perinereis nigropunctata Horst, 1924 [1]		11					
unidentified polychaetes	2	6		1	4	3	
B Enteropneusts							
Ptychoderidae							
Ptychodera flava Eschscholtz, 1825							1
Total identified food	7	23	1	3	5	5	2
unidentified food	0	0	0	0	5	0	5

[1] tentative identification

C. coronatus, C. ebraeus, C. miliaris and *C. rattus*. The polychaetes in the diets of *C. flavidus, C. lividus,* and *C. sanguinolentus* were mainly from the sedentary families Ampharetidae, Capitellidae, Cirratulidae, Maldanidae, and Terebellidae. Exceptions were two *C. flavidus,* each of which had eaten the eunicid *Palola siciliensis,* two *C. sanguinolentus,* each containing a phyllodocid and one *C. ebraeus* which was found to have eaten the capitellid *Dasybranchus cadacus.*

The only marked difference in dietary composition between the samples of the same species from Lady Elliot Island and Low Isles was for *Conus ebraeus.* Of the 83 prey animals identified from Lady Elliot Island 76% were eunicids and 7% nereids, while at Low Isles the diet comprised 48% nereids and 26% eunicids.

(5) PREY SPECIFICITY

Indices of prey species diversity (H) and prey specificity (R) for 5 species of *Conus* at Lady Elliot Island and one species at Low Isles are presented in Table 5. The information obtained from the other species was insufficient for this type of analysis.

Table 5

Prey species diversity and redundancy of *Conus* on the reef crest.

Species	Prey species diversity H	Prey species redundancy R	Number of prey species eaten	Number of prey organisms identified
A Lady Elliot Island				
Conus				
coronatus	1.1541	0.1676	4	18
ebraeus	0.3095	0.7768	4	67
flavidus	1.2178	0.4144	8	53
sanguinolentus	1.0334	0.0593	3	11
miliaris	0.6804	0.0183	2	19
B Low Isles				
ebraeus	0.8095	0.2809	3	17

The indices of prey species overlap (R_o), calculated for all pairings of the Lady Elliot Island species in Table 5, are presented in matrix form in Table 6.

Table 6

The indices of prey species overlap R_o calculated for all pairings of five species of *Conus* at Lady Elliot Island.

Conus	*coronatus*	*ebraeus*	*flavidus*	*sanguinolentus*
ebraeus	0.61			
flavidus	0.10	0.16		
sanguinolentus	0.00	0.00	0.00	
miliaris	0.85	0.75	0.12	0.00

Of the species studied at Lady Elliot Island *Conus flavidus* had the most diverse diet as measured by both H and the number of prey species eaten. *Conus ebraeus* had the diet with the lowest diversity and highest redundancy at this locality. However, at Low Isles nereids comprised a greater proportion of the diet of *C. ebraeus* and its diet was both more diverse and less redundant than at Lady Elliot Island.

Reference to Table 6 shows that the species which ate sedentary polychaetes, *Conus flavidus* and *C. sanguinolentus* had little or no dietary overlap with any of the other species at Lady Elliot Island. In contrast, the species feeding on eunicids and nereids, *C. ebraeus, C. coronatus* and *C. miliaris* had fairly similar diets and the R_os for the various pairings of these species were all greater than 0.6.

DISCUSSION

Gut-content analyses of 887 vermivorous *Conus* yielded 307 specimens of prey of which 265 were identified. All the *Conus* studied fed on polychaetes, *C. sanguinolentus* eating enteropneusts as well. Comparison of the food of *Conus* from Hawaii (Kohn, 1959), Ceylon (Kohn, 1960), the Maldive and Chagos Islands (Kohn, 1968) and the Great Barrier Reef shows that the diets of various species of *Conus* are remarkably constant. For example, *Palola siciliensis* is a major food item of *C. ebraeus* at Hawaii, Maldive and Chagos Islands and at Lady Elliot Island. However, bioassay studies suggest that within the vermivorous Conidae prey specificity is not reflected in venom specificity. Marsh (1970) found that the venoms of 5 species of *Conus* affected *P. siciliensis* even though it was a prey animal of only 3 of them.

Field evidence shows that the prey of vermivorous *Conus* is not necessarily paralysed. As the capture of prey was not observed, it is not known whether, in these cases, the prey was stung. In the laboratory the stinging of prey is not essential to feeding in vermivorous cones (Kohn, 1959; Marsh, 1970; Saunders & Wolfson, 1961). Bioassay work (Marsh, 1970) to test the effect of the venom of *C. chaldeus, C. ebraeus, C. flavidus, C. lividus* and *C. miliaris* on *Palola siciliensis* showed that the effect of the venom was to inhibit the polychaete's response to stimulation and to render it incapable of normal progression rather than to paralyse it. Only the venom of *C. lividus* caused paralysis, but this was limited to a few segments in the region of injection.

Kohn (1966) presents evidence that for the genus *Conus* increased food specialization is associated with increased numbers of taxonomically and ecologically sympatric species. *Conus californicus* Hinds, 1844, the only species of *Conus* occurring in southern California has a far more diverse ($H = 2.82$ and less redundant ($R = 0.12$) diet than do the species which occur on Hawaii and Maldive and Chagos coral reefs where there are large numbers of sympatric species of *Conus*. Twenty-one species of *Conus* were recorded from the reef crest at Lady Elliott Island and 13 from the crest at Low Isles. The diets of the vermivorous *Conus* from these areas were also characterised by low diversity and high redundancy compared with *C. californicus*. It is also notable that at Lady Elliot Island the 2 species with lowest prey species overlap, *C. flavidus* and *C. sanguinolentus* had the most diverse and least redundant diets. Thus, species of *Conus* which co-occur and exploit the same set of resources are more specialised in diet than *C. californicus*.

SUMMARY

1. Twenty-one species of *Conus* were collected from the reef crest at Lady Elliot Island and 13 species from the crest at Low Isles.
2. The size distribution and sex ratios of the most common vermivorous *Conus* were calculated.
3. Feeding was shown to take place mainly at night for *Conus flavidus* while *Conus ebraeus* appeared to feed at least until mid-morning.
4. Field evidence was obtained that the prey of vermivorous *Conus* is not always paralysed.
5. All the *Conus* studied fed exclusively on polychaetes

except *Conus sanguinolentus* which ate enteropneusts as well.

6. The diets of the species studied were characterized by low diversity and high redundancy.

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